The phylogenetic relationships of the Dodo (*Raphus cucullatus*) and the Solitaire (*Pezophaps solitaria*) within Columbidae (Aves: Columbiformes), including other large extinct taxa, based on morphological data

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Abstract
The phylogenetic position of the Dodo (*Raphus cucullatus* (Linnaeus 1758)) and Solitaire (*Pezophaps solitaria* (Gmelin 1789)), the large extinct pigeons of the Mascarene Islands, has been determined by analysis of molecular and morphological data. However, robust and concordant phylogenetic relationships of these taxa have not been satisfactorily determined using morphological data. Furthermore, several other large extinct terrestrial columbids have not been included in any previous analyses – either morphological or molecular – precluding robust knowledge of their relationships. A new parsimony analysis was undertaken, utilizing 32 columbid taxa (including the extinct taxa *Bountyphaps* Worthy & Wragg 2008, *Microgoura* Rothschild 1904, *Natunaornis* Worthy 2001, *Gallicolumba nui* Steadman 1992 and *G. longitarsus* Balouet & Olson 1989) and 140 osteological, soft-part and behavioural characters. The results of the present analysis support the findings of Janoo and Shapiro *et al*. in the placement of the Dodo and Solitaire close to *Goura* Stephens 1819, and of the latter authors' analysis in recovering similar clades. Differences in the results may be due to the effects of homoplasy (convergence towards terrestriality and large size) and heterochrony (paedomorphism and peramorphism), which played an important part in the evolution of the Dodo and Solitaire.

Introduction
The Dodo (*Raphus cucullatus* (Linnaeus 1758)) and the Solitaire (*Pezophaps solitaria* (Gmelin 1789)) (see Figure 1 for illustration), extinct columbiformes from the Mascarene Islands, are well known and have been the subject of numerous studies (Claessens *et al*. 2015; Hume 2006; Janoo 1996; Lüttschwager 1959; Parish 2013; Strickland & Melville 1848). A columbiform placement of the Dodo was first recognized by Johannes Theodore Reinhardt in 1843 (Parish 2013) and has subsequently been confirmed by morphological parsimony analysis (Livezey & Zusi 2006, 2007).

There have been a number of previous phylogenetic analyses – both morphological and molecular – incorporating the Dodo and Solitaire. The sister taxon relationship of *Raphus* Brisson 1760 and *Pezophaps* Strickland 1848 has been confirmed by both morphological (Janoo 2000) and molecular (Pereira *et al*. 2007; Shapiro *et al*. 2002) studies. The closest living relatives of *Raphus* and *Pezophaps* have been determined as either *Goura* Stephens 1819 (Janoo 2000) or *Caloenas* G. R. Gray 1840 (Besnard *et al*. 2016; Bruxaux 2018; Bruxaux *et al*. 2018; Chen *et al*. 2022; Fulton *et al*. 2012; Heupink *et al*. 2014; Lapiedra *et al*. 2013; Oliver *et al*. 2023; Pereira *et al*. 2007; Shapiro *et al*. 2002; Soares *et al*. 2016). However, several extinct large to giant taxa, such as *Bountyphaps obsoleta* Worthy & Wragg 2008 (Henderson Island and islands in the Gambier Group), *Microgoura meeki* Rothschild 1904 (Solomon Islands) and *Natunaornis gigoura* Worthy 2001 (Viti Levu, Fiji), in addition to some species currently placed in *Gallicolumba* (*G. longitarsus* Balouet & Olson 1989 (New Caledonia) and *G. nui* Steadman 1992b (Marquesas, Society Islands? and Cook Islands?)), have never been analysed phylogenetically, let alone in combination with *Raphus* and *Pezophaps*. The present study aims to determine the phylogenetic relationships of these large extinct columbids using parsimony analyses of morphological data, and to place the Dodo and Solitaire within an evolutionary context.

The only previous morphological phylogenetic analyses to include the Dodo and Solitaire were those of Janoo (1997, 2000), Livezey & Zusi (2006, 2007) and Parish (2013; the data set of which is unavailable). Those of Janoo contained a number of errors (see Appendix 1). In addition, a number of key taxa of interest were omitted, including the terrestrial pigeons *Microgoura* Rothschild 1904, *Otidiphaps* Gould 1870 and *Trugon* G. R. Gray 1849. The analysis of Livezey & Zusi was limited in that it only contained eight columbid taxa (*Raphus*, *Pezophaps*, *Columba* Linnaeus 1758, *Didunculus* Peale 1849, *Ducula* Hodgson 1836, *Geopelia* Swainson 1837, *Goura* and *Zenaida* Bonaparte 1838). Moreover, it also contained coding errors (Mayr 2008; pers. obs.). Since Janoo's analysis, several further taxa of interest have been described. To address these deficiencies a broad sample of columbid taxa was made, with special focus on those having been placed close to the Dodo and Solitaire (either through cladistic analyses or by more general comparisons), including two of the recently described flightless and extinct insular taxa: *Bountyphaps obsoleta* and *Natunaornis gigoura*, the latter almost as large as the Dodo. In addition, the Holocene extinct taxa '*Gallicolumba*' *longitarsus*, and '*G*'. *nui* were also included (on account of their size, likely terrestrial habits, and morphological features differing from those of all other species of *Gallicolumba* Heck 1849 (and *Pampusana* Bonaparte 1855b)), as well as the Miocene *Rupephaps taketake* Worthy *et al*. 2009 from New Zealand.

Materials and methods
Nomenclature

Clade names follow Young *et al*. (2024). Clades are here defined as follows: Raphini: those taxa closer to *Raphus cucullatus* than to either *Ptilinopus regina* Swainson 1825 or *Phaps chalcoptera* (Latham 1790). Ptilinopodini (Ptilinopinae of Worthy *et al*. 2009): those taxa closer to *Ptilinopus regina* than to *Raphus cucullatus*. Phabini (Phabinae of Worthy 2012): those taxa closer to *Phaps chalcoptera* than to either *Raphus cucullatus* or *Ptilinopus regina*. Osteological nomenclature follows Baumel & Witmer (1993).

Columbid taxonomy

The nomenclature of columbids follows Dickinson & Remsen (2013) with the following exceptions:
Columba species assignment following Johnson *et al*. (2001). No species of *Patagioenas* Reichenbach 1853 were included in the present study.
Gallicolumba species assignment following Moyle *et al*. (2013). No species of *Pampusana* (formerly *Alopecoenas* Sharpe 1899) were included in the present study.
Megaloprepia magnifica (Temminck 1821) is used for *Ptilinopus magnificus* as advocated by Cibois *et al*. (2014).
Nesoenas Salvadori 1893 is used for the Mascarene turtledoves formerly in *Streptopelia* Bonaparte 1855a, as advocated by Cheke (2005), following Johnson *et al*. (2001).
Nyctiperdix Roberts 1922 species assignment following Cohen (2011).
Ptilinopus Swainson 1825 species assignment following Cibois *et al*. (2014).

Abbreviations

AMNH: American Museum of Natural History, New York, USA
BP = Before Present (Present = 2004 CE)
BPBM: Bernice P. Bishop Museum, Honolulu, USA
CI: ensemble Consistency Index
FlMNH: Florida Museum of Natural History, Gainesville, USA
MPT: Most Parsimonious Tree NMNZ: Museum of New Zealand (Te Papa Tongarewa), Wellington
QM: Queensland Museum, Brisbane, Australia
RI: ensemble Retention Index
SAM: South Australian Museum, Adelaide, Australia
SMF: Forschungsinstitut Senckenberg, Frankfurt am Main, Germany
TNT: Tree Analysis Using New Technology (Goloboff *et al*. 2008)
Tring: Natural History Museum, Tring, Hertfordshire, UK
UF: University of Florida, USA
UMZC: University Museum of Zoology, Cambridge, UK
USNM: United States National Museum, Washington, D. C., USA

Extinct taxa included

The following extinct taxa were also included in addition to the Dodo and Solitaire:

● *Natunaornis gigoura* was described from Quaternary sites on Viti Levu, Fiji, by Worthy (2001), who noted that "some characters of the tarsometatarsus, tibiotarsus, and humerus are closer to *Goura* than to any other taxon" (p.763).
● *Bountyphaps obsoleta* was described from archaeological sites on Henderson Island, Pitcairn Group (Worthy & Wragg 2008). Later, Rigal *et al*. (2018) identified this species from Agakauitai and Kamaka Islands, Gambier Group, and proposed that specimens from Kamaka Island, that were previously referred to *Gallicolumba nui* by Steadman & Justice (1998), were more likely *B. obsoleta*. However, Rigal *et al*. stated that caution should be taken in considering *Bountyphaps* as native to Kamaka and Agakauitai Islands, and put forward the possibility that the genus might have been introduced there by Polynesian colonizers.
● *Didunculus placopedetes* Steadman 2006a was described from subfossil bones (*c*.2850 cal BP) from 'Eua and Tongatapu, Kingdom of Tonga (Steadman 2006a), and its range was extended to Efate, Vanuatu (2500–3000 years BP) by Worthy *et al*. (2015), and to Tongatapu, Ofu Island and Pangaimotu Island, Kingdom of Tonga, by Worthy & Burley (2020). It was 20–25% larger in linear skeletal measurements than *D. strigirostris* (see Steadman 2006a).
● *Gallicolumba longitarsus* was described from apparently Holocene deposits in Pindai Cave, New Caledonia (Balouet & Olson 1989). The holotype comprises a left tarsometatarsus (MNHN NCP 100), with paratypes including a left femur (MNHN NCP 101) and a partial left coracoid (MNHN NCP 105). It was assigned to *Gallicolumba* as "*Gallicolumba* is the only genus of Columbidae in Australasia and Oceania with the tarsometatarsus extremely elongated" (Balouet & Olson 1989, p.16). However, '*G*'. *longitarsus* differs from all other species of *Gallicolumba* (and *Pampusana*) in having a pneumatic foramen on the cranial face of the femur (*ibid*.) – a feature seen in raphin taxa. It also has a lower femur to tarsometatarsus length ratio (0.88, compared to 0.95 or greater for *Gallicolumba* and *Pampusana*).
● *Gallicolumba nui* was described from archaeological deposits on Ua Huka, Hiva 'Oa and Tahuata, Marquesas Islands (Steadman 1992b), with specimens subsequently referred to this species from Huahine, Society Islands, and Mangaia, Cook Islands (Steadman 1992b; Steadman & Takano 2020). The holotype and paratype tarsometatarsi were assigned to *Gallicolumba*, rather than to *Caloenas*, *Chalcophaps* Gould 1843, *Columba*, *Didunculus*, *Ducula*, *Macropygia* Swainson 1837 or *Ptilinopus* due to "overall shape narrow and elongate; intercondylar tuberculum large; foramina vascularia proximalia small; proximomedial portion of the shaft shallow in medial aspect; proximodorsal surface of

shaft not highly excavated; plane of trochleae highly curved in distal aspect" (Steadman 1992b, p.330). However, it differs from *Gallicolumba* (and *Pampusana*) in several characters, including pneumatic foramina under the acrocoracoid process of the coracoid, a centrally- (as opposed to medially-) located pneumatic fossa in the sternocoracoid impression of the coracoid (a feature seen in raphin taxa; as shown in Figure 7), and pneumatic foramina in the incisura capitis of the humerus.

● *Rupephaps taketake* is known from a left coracoid and referred right tarsometatarsus from the St Bathans Fauna (Early Miocene) of New Zealand (De Pietri *et al*. 2017; Worthy *et al*. 2009). De Pietri *et al*. (2017) placed *Rupephaps* as the sister-taxon to the clade comprising *Gymnophaps* Salvadori 1874, *Lopholaimus* Gould 1841 and *Hemiphaga* Bonaparte 1854.

Phylogenetic analyses

A parsimony-based cladistic analysis was undertaken, using 32 mainly genus-level columbid taxa. Megapodiidae (based on data from *Alectura lathami* J. E. Gray 1831, with additional data from other megapodiid taxa) was chosen as the outgroup, being the basalmost extant family of Galliformes (Galliformes being a member of Galloanseres, the sister taxon to Neoaves). Mesitornithidae (*Mesitornis unicolor* (Des Murs 1845), *Me. variegatus* Geoffroy Saint-Hilaire 1838, *Monias benschi* Oustalet & Grandidier 1903) was chosen as the proximal outgroup based on the molecular studies of Hackett *et al*. (2008), Yuri *et al*. (2013), Jarvis *et al*. (2014), Prum *et al*. (2015), Reddy *et al*. (2017) and Stiller *et al*. (2024). Of the columbids fourteen were the sole representatives of their genera (not including '*Gallicolumba*' *longitarsus* and '*G*.' *nui*). However, sixteen genus-level taxa were scored from multiple species (*Alectroenas* G. R. Gray 1840, *Caloenas* (including *C. nicobarica* (Linnaeus 1758) and the extinct *C. maculata* (Gmelin 1789)), *Chalcophaps*, *Columba*, *Didunculus* (including *D. strigirostris* (Jardine 1845) and the extinct *D. placopedetes*), *Ducula*, *Gallicolumba*, *Geopelia*, *Geophaps* G. R. Gray 1842, *Goura*, *Macropygia*, *Nesoenas*, *Phaps* Selby 1835, *Ptilinopus*, *Streptopelia*, and *Treron* Vieillot 1816; Appendix 2). The monotypic columbid taxa included nine monotypic extinct species: *Raphus cucullatus*, *Pezophaps solitaria*, *Bountyphaps obsoleta*, *Ectopistes migratorius* (Linnaeus 1766), '*Gallicolumba*' *longitarsus*, '*G*.' *nui*, *Microgoura meeki*, *Natunaornis gigoura*, and *Rupephaps taketake*. A total of 140 osteological, soft-part and behavioural characters were coded, including fourteen continuous and 126 discrete characters. Taxa were coded from examination of specimens, from the literature and from other sources (see Appendix 2 for material examined; Appendix 3 for notes on coding). Behavioural characters were also included, as in Dyke *et al*. (2003), and in coding characters the observations of Sereno (2007) were taken into account. Discrete data were compiled using Mesquite Version 2.75 (build 564; Maddison & Maddison 2011) and combined with the continuous data in a .tnt file (see Supplementary files).

The parsimony analyses were run using TNT Version 1.6 (Willi Hennig Society edition, Linux GUI version; Goloboff & Catalano 2016; Goloboff & Morales 2023; Goloboff *et al*. 2008). The max. trees setting was increased to 99,999. Branches with no possible support (maximum length = 0) among any of the recovered MPTs were collapsed (rule 3 of Swofford & Begle 1993). Megapodiidae was set as the outgroup. A New Technology search, using sectorial search, ratchet, drift and tree fusing options and ten random addition sequences, was performed. In order to find all the Most Parsimonious Trees (MPTs), this was followed by a round of tree bisection-reconnection (TBR) using the Traditional Search option, with one random addition seed, 1000 replications and 100 trees saved per replication. Continuous characters are treated as ordered (additive) in TNT and are automatically rescaled (Raven & Maidment 2017). All characters were unweighted. In order to investigate support for the relationships identified by the analyses, bootstrap analysis (10000 replicates) and symmetric resampling (10000 replicates, 33% change probability) were carried out using traditional searches in TNT. Bremer support values were also calculated.

First, analyses were carried out with no constraints employed. Subsequent analyses used a constraint tree to constrain the relationships of taxa to those well-established from molecular analyses using mitochondrial genome data. This was done so that the relationships of the other included fossil taxa could be determined from their morphological data in the context of known columbid phylogenetic relationships. The molecular constraint tree (see Supplementary files) was based on the maximum clade credibility tree of Bruxaux (2018), figs.22, 25). The Bruxaux tree was chosen as it included a large number of taxa, particularly those of interest (considered to be closely related to the Dodo and Solitaire), represented by mitochondrial genomes. Following Jarvis *et al*. (2014), Prum *et al*. (2015) and Reddy *et al*. (2017), Megapodiidae was added to the Bruxaux tree as the most distant outgroup, and a clade of Pterocliformes+Mesitornithiformes was placed as the immediate sister-taxon to the columbid ingroup. The extinct taxa *Bountyphaps*, *Natunaornis* Worthy 2001, '*Gallicolumba*' *longitarsus*, '*G*'. *nui* and *Rupephaps* were set as 'floating' taxa, due to their absence from the constraint tree. The data set was then re-analysed with constraint tree enforced, thereby allowing these extinct taxa to be placed as the data dictated.

A reduced data set, comprising thirteen raphin taxa (as determined by the results of the above-mentioned constrained analysis), with the addition of *Columba* (outgroup), *Ducula* and *Starnoenas* Bonaparte 1838, coded for 113 osteological, soft-part and behavioural characters (comprising fifteen continuous and 98 discrete characters), was also investigated. As the data set contained only a small number of taxa, a branch-and-bound (implicit enumeration) search was performed. A constraint tree was then utilized to enforce the topology of the Bruxaux tree to the Raphini data set,

with *Bountyphaps obsoleta*, *Natunaornis gigoura*, *Didunculus placopedetes*, '*Gallicolumba*' *longitarsus* and '*G*'. *nui* set as 'floating' taxa, and a branch-and-bound search performed.

Taxa not included in the present analyses

There are several other extinct and fossil columbid taxa, whose relationships have not been phylogenetically examined and which may potentially have a close relationship with the Dodo and Solitaire: *Caloenas canacorum* Balouet & Olson 1989, *Deliaphaps zealandiensis* De Pietri *et al*. 2017, *Dysmoropelia dekarchiskos* Olson 1975, *Pampusana leonpascoi* (Worthy & Wragg 2003), *Primophaps schoddei* Worthy 2012, and *Tongoenas burleyi* Steadman & Takano 2020. Due to insufficient data the following extinct and fossil columbids were not included in the analyses.

● *Caloenas canacorum*, known from Holocene remains from New Caledonia, was around 25% larger than *C. nicobarica*. Balouet & Olson (1989) estimated the total length, bill to tail tip, to be around 38 cm, although they stated that there was no indication of a reduction in flight capability compared with *C. nicobarica*. Specimens assigned to *Caloenas* sp. from the Vava'u Group, The Kingdom of Tonga, were described by Worthy & Burley (2020) and bones from Lifuka, Tonga, were assigned to *C. canacorum* by Steadman (1989) and Steadman & Takano (2020). However, the tarsometatarsus assigned to *C. canacorum* (UF 158508) is more elongated than that of either *C. nicobarica* or *C*. sp., being more like that of '*Gallicolumba*' *nui* in its length to proximal width ratio. Coding the available data for *Caloenas canacorum* and adding it to the Raphini matrix resulted in it being placed basal to *Goura+Didunculus* when analysed with the constraint tree enforced.
● *Deliaphaps zealandiensis* is recorded from the St Bathans Fauna (19–16 Ma), New Zealand (De Pietri *et al*. 2017). The holotype carpometacarpus displays a combination of features seen in *Caloenas nicobarica*, *Didunculus strigirostris* and *Goura cristata* ([Pallas] 1764) (*ibid*.).
● *Dysmoropelia dekarchiskos* is known only from late Pleistocene remains from Saint Helena, dating from approximately 14,000 years BP (Lewis 2008). The facies articularis clavicularis of the coracoid is not hooked. The well-developed brachial fossa of the humerus extends slightly more proximally than the level of the dorsal supracondylar process. Olson (1975) concluded that *Dysmoropelia* was probably flightless and from comparison with numerous other columbid specimens found it to have greatest affinity with *Streptopelia*. Thus, *Dysmoropelia* does not appear to be closely related to the flightless columbids of the Mascarene Islands.
● *Pampusana leonpascoi* (originally *Gallicolumba leonpascoi*) is known from late Pleistocene to Holocene deposits on Henderson Island, Pitcairn Group. Worthy & Wragg (2003) considered it to be most closely related to *Pampusana stairi* (G. R. Gray 1856) and *P. rubescens* Vieillot 1818 and noted that "[r]elatively enlarged leg elements and reduced wing elements suggest that this dove was facultatively flightless" (p.769). Coding the available data for *Pampusana leonpascoi* and adding it to the matrix resulted in it being placed as sister taxon to *Phaps* when analysed with the constraint tree enforced. *P. leonpascoi* was excluded from the analysis due to paucity of data and the absence of *Pampusana* in the data set.
● *Primophaps schoddei* is known from a left coracoid from the Late Oligocene deposits at Riversleigh, Queensland (Worthy 2012). Worthy (2012) considered it to be a phabin.
● *Tongoenas burleyi* is recorded from Holocene and late Pleistocene sites on the Tonga Islands: Foa, Lifuka, 'Uiha, Ha'afeva, Tongatapu and 'Eua (Steadman & Takano 2020). It was a large pigeon; Steadman & Takano (2020) stated that "[a]mong volant columbids, living or extinct, *Tongoenas burleyi* is exceeded in size only by the species of *Goura*" (p.408). It was considered by Steadman & Takano (2020) to be most closely related to *Ducula*, *Drepanoptila* Bonaparte 1855c, *Gymnophaps*, *Hemiphaga* and *Ptilinopus*. Coding the available data for *Tongoenas* and adding it to the matrix resulted in it being placed as sister taxon to *Rupephaps* in a clade with *Treron* and *Chalcophaps* when analysed with the constraint tree enforced.
● An unnamed 'columbid' from the middle Miocene Tsurushi Formation of Niigata Prefecture, Japan, was described by Ono & Uyeno (1985). The specimen consists of a near complete but flattened skeleton, lacking the rostral part of the skull, some vertebrae, the wings and pectoral apparatus, part of the pelvis, and parts of the hindlimbs. The tarsometatarsus would appear to be around 30 mm in length (from the scale bar given in the published photograph). However, its affinities, and even its columbiform status, are uncertain.

For reasons stated above, most of these taxa are not considered likely to be close relatives of *Raphus* and *Pezophaps* and thus not central to the aims of this paper. Three of these taxa (*Caloenas canacorum*, *Pampusana leonpascoi* and *Tongoenas burleyi*) were added individually to some analyses, but due to paucity of available data were excluded from the main taxon set.

The TNT files and character lists can be found in the supplementary information.

Results

Columbiformes dataset (unconstrained analysis)

The parsimony analysis of the unconstrained Columbiformes data set yielded four MPTs (best score: 484.379, CI 0.33, RI 0.56; shown in Figure 2) in which several separate clades were resolved. *Raphus* and *Pezophaps* are placed in a clade containing other large, terrestrial taxa. A clade comprising fruit pigeons (Ptilinopodini) was also recovered, as was

a group comprising phabin pigeons. '*Gallicolumba*' *nui* was placed among raphins, rather than nesting with *Gallicolumba*, although '*G*.' *longitarsus* was placed in a basal polytomy with *Microgoura* and other taxa. *Otidiphaps* and *Trugon* were also placed together in a clade. *Rupephaps* was placed as sister-taxon to *Lopholaimus*, concordant with the hypothesis of De Pietri *et al*. (2017). Bootstrap, symmetric resampling and Bremer support values are given in Appendix 4. Running the data with continuous characters excluded (inactive) produced twelve MPTs (score 447, CI 0.33, RI 0.57). The strict consensus of these showed improved resolution compared with the analysis of the full character set, but resulted in several taxa being placed differently (including '*Gallicolumba*' *longitarsus* being placed within Raphini), although similar clades were recovered (see Appendix 4).

Columbiformes dataset (with Bruxaux 2018 constraint)
Analysis of the data constrained using the backbone based on Bruxaux (2018), figs.22, 25) yielded one tree (best score: 547.150, CI 0.29, RI 0.47; shown in Figure 3). The placement of the subfossil taxa differs from that of the unconstrained analysis in that '*Gallicolumba*' *longitarsus* was placed as sister-taxon to *Microgoura*.

Raphini dataset (unconstrained analysis)
The analysis of the unconstrained Raphini data set yielded two MPTs (best score: 223.880, CI 0.54, RI 0.53; shown in Figure 4). *Starnoenas* was resolved within Raphini, being in a clade with *Microgoura*, *Trugon* and *Otidiphaps*. '*Gallicolumba*' *longitarsus* was resolved as the sister-taxon to *Microgoura* and '*Gallicolumba*' *nui* was placed as more derived than *Caloenas*. Running the data with continuous characters excluded (inactive) produced 36 MPTs (score 205, CI 0.54, RI 0.52), the strict consensus of which showed markedly decreased resolution compared with the analysis of the full character set (see Appendix 4). Much of this loss of resolution appears to be the result of the instability of *Microgoura*.

Raphini dataset (with Bruxaux 2018 constraint)
Analysis of the Raphini dataset using the Bruxaux (2018) constraint tree yielded one tree (best score: 241.000, CI 0.50 RI 0.45; shown in Figure 5).

Natunaornis from Viti Levu was resolved as the sister taxon to the Mascarene *Raphus* and *Pezophaps*, as it is in all the analyses. '*Gallicolumba*' *nui* and *Bountyphaps* inserted as successive sister taxa to the Mascarene taxa to the exclusion of *Caloenas*. As is the case with the constrained Columbiformes analysis, '*Gallicolumba*' *longitarsus* was resolved sister to *Microgoura*, far from *Gallicolumba sensu stricto*. The clade *Natunaornis* (*Raphus*+*Pezophaps*) is supported by a lack of a hook on the clavicular articular face of the coracoid (43) and a rounded-off deltopectoral crest (63).

The clade '*Gallicolumba*' *nui* > *Raphus* is supported by the following characters: procoracoid lobe of the coracoid does not extend craniad of the scapular cotyla (48), medial angle of the coracoid is acute (51), humeral head does not project, or projects only slightly, beyond a line marking the proximal margin of incisura capitis (64) and the pisiform process of the carpometacarpus located at approximately the same level as the extensor process (70). '*Gallicolumba*' *longitarsus* and *Microgoura* are united by the ratio of tarsometatarsal length to proximal width (13). Raphini itself is supported by a single synapomorphy: lateral retinaculum m. fibularis of the tibiotarsus aligned craniocaudally (80).

Discussion
In both the unconstrained and constrained results *Raphus* and *Pezophaps* were placed in a clade containing other large, terrestrial taxa, in accordance with previous results from molecular data.

The unconstrained Columbiformes analysis yielded clades comprising fruit pigeons (Ptilinopodini) and phabin pigeons – both of which are in accord with molecular data, albeit differing in their arrangement. The placement of '*Gallicolumba*' *longitarsus* and '*G*.' *nui* among raphins, and not with *Gallicolumba*, confirms that they do not belong in *Gallicolumba*, though this analysis did not include any of the taxa formerly in *Gallicolumba* but presently placed in *Pampusana*.

In the unconstrained analyses, *Raphus* and *Pezophaps* are resolved as sister-taxa within Raphini, their closest relatives being *Natunaornis* and *Goura*. This placement as being closely related to *Goura* is in agreement with previous results for morphological (Janoo 2000; Livezey & Zusi 2007) and molecular (*e.g*., Chen *et al*. 2022; Shapiro *et al*. 2002) analyses. However, there are differences in tree topology between these results and those of previous analyses. These differences may be due to the taxa and characters used, and the accuracy of the data set in the case of morphological data. In addition, convergence in increased body size and terrestriality could be causing taxa to group together in the present morphological analysis. Indeed, the geographical distribution of taxa suggests that this may be the case: *Raphus* and *Pezophaps* are Indian Ocean taxa (*Caloenas nicobarica* is found on islands from India east through Indonesia to the Solomon Islands and Palau), whereas their sister taxon, *Natunaornis*, is found in the Pacific (Fiji). All raphins are insular (although some are found on large islands, such as New Guinea), and this is further suggestive of the significance of convergent evolution, as insular avian taxa often evolve increased terrestriality (Wright *et al*. 2016).

Character complexes may also be part of the issue, with groups of characters related to terrestriality and flight loss strengthening the effects of convergence.

Due to the effects of convergence, with taxa not closely related having similar morphologies due to occupying similar ecological niches, the preferred trees are those with the molecular constraint.

Convergence towards increased terrestriality is herein suspected to be common within Columbidae, and is seen in diverse taxa such as *Dysmoropelia*, *Gallicolumba* and the raphins. This convergence may also be more frequent within Raphini, but may not be apparent in the results due to the phylogenetic signal being overwhelmed by homoplastic characters. The employment of a constraint tree, based on the molecular results of Bruxaux (2018) allows some degree of investigation of potential convergence.

Columbids have a tendency to become larger and more terrestrial, with flightlessness developing in certain cases. Worthy (2001) noted that *Raphus* and *Pezophaps* "were slightly larger than *Natunaornis*, but differed substantially in morphology and so are not closely related" (p.791). He considered the latter to be closer to *Goura*. The placement of *Natunaornis* as sister taxon to *Raphus+Pezophaps* in the present analyses may be due to a combination of the fragmentary nature of the specimens of the former and convergence, with all three taxa being large, terrestrial and having limited or no capacity for flight. The larger the bird, the more accessible foods such as large fruits and seeds become. A flightless bird is able to expend more energy on digestion and can develop a large digestive system. *Raphus* and *Pezophaps* both have a long and wide postacetabular region and a bowl-like sternum, suggesting the presence of a large gut and significant post-oral processing of food. *Raphus* was named 'dronte' ('swollen') by Dutch explorers, and Leguat (1708, p.71) said of *Pezophaps*: "their Hind-part [...] is Roundish, like the Crupper of a Horse". This large gut likely allowed exploitation of otherwise unavailable food resources, especially during times of food scarcity. Thus, size increase may be linked to a convergent similarity in morphology of those elements connected with feeding and locomotion.

The difference in topology between the results of the unconstrained analyses and the results of molecular analyses suggests that a certain degree of convergence has indeed taken place, with taxa developing increased terrestriality. This has led to convergent taxa grouping together in the morphological analysis, with the large terrestrial *Goura* being placed close to *Raphus* and *Pezophaps*. In molecular analyses *Caloenas* is closer to *Raphus* and *Pezophaps* than *Goura* is. Unfortunately, molecular data has not been obtained for *Bountyphaps* or *Natunaornis* (which are only known from specimens from archaeological sites). The more closely related taxa are, and therefore the fewer the differences between them, the more significant convergently acquired characters become. This is a problem for standard morphological analyses (*e.g.*, A. J. Baker *et al*. 2014; Garcia-R *et al*. 2014; Yonezawa *et al*. 2017) and it may be that molecular analyses are the only way to accurately elucidate raphin phylogeny.

The placement of *Microgoura* close to *Trugon* is supported by Gibbs *et al*. (2001), who stated that "[i]ts closest relative is probably *Trugon*" (p.418). Both have similar plumage (upper mantle greyish, wing-coverts brown, primaries brown, abdomen rich ochre to bright cinnamon with distinct demarcation between this and the grey chest, back to upper tail grey or greyish brown), reddish tarsi and are of similar size (wing: *Microgoura* ♂195–197 mm ♀*c*.180–190 mm, *Trugon* ♂175–180 mm ♀165–171 mm; tail: *Microgoura* 100–105 mm, *Trugon* 95–127 mm) (Gibbs *et al*. 2001; Rothschild 1904). Steadman & Takano (2020) remarked that "[t]he tibiotarsus and tarsometatarsus of *Microgoura* are [...] nearly indistinguishable from those of *Trugon*" (p.404).

The placement of *Microgoura*, *Otidiphaps*, *Trugon*, *Gallicolumba* and *Starnoenas* basal to Raphini, Ptilinopodini and Phabini in the unconstrained Columbiformes analysis is also likely to be an artefact, as it conflicts with the molecular studies. The effects of heterochrony may be causing taxa to be placed incorrectly. Derived taxa can exhibit plesiomorphic features due to paedomorphosis and so be placed lower down in the tree than is actually the case (Struck 2007). However, without a comprehensive knowledge of ontogenetic development of taxa the potential effects of heterochrony are difficult to ascertain. Similarly, characters linked to terrestriality may also be causing the Raphini to be resolved as more basal than is actually the case due to the outgroup taxa (Megapodiidae, Mesitornithidae and Pteroclidae) also being terrestrial.

In addition to these, there are further inherent problems of taxon-character matrices, as discussed by Vermeij (1999). Sookias (2019), in his analysis of crocodilian taxa, found that meristic characters were more homoplastic than non-meristic ones. He noted that "[m]eristic characters can appear attractive [for inclusion in phylogenetic analyses] because of their clear, natural delimitation. However, most such characters pertain to serial homologues (e.g. teeth, vertebrae), which tend to increase in number if the structure in which they are embedded or which they form increases in length or size" (p.695). Sookias added that meristic characters "do seem to be exceptionally labile, probably because of the ease of shifting the mechanisms controlling these characters, e.g. the speed of the 'segmentation clock' regulating somitogenesis and shifting *Hox* gene expression regions controlling regionalization [...], without greatly impeding function or interfering with development of other structures" (p.695). Thus, for example, the numbers of different vertebrae in birds may be less phylogenetically informative than other, non-meristic, characters. Similarly, as a

reduction in the lengths of distal wing elements is related to flight loss (Nudds & Davidson 2010; Watanabe 2017), ratios based on these may also be less phylogenetically informative than other characters due to the effects of homoplasy.

Conflict between the morphological and molecular trees regarding the relationships of taxa within non-raphin clades is likely due to a lack of included apomorphies relating to those clades; the focus of this paper being the phylogenetic placement of the Dodo and the Solitaire, rather than a complete phylogeny of Columbiformes.

Biogeography

Columbiformes have a global distribution, found on all continents with the exception of Antarctica. The biogeographical distribution of raphins is shown in Figure 6. As can be seen, their distribution is either Pacific Ocean/Australasian or Indian Ocean, with their phylogenetic arrangement suggesting that they dispersed to the latter from the former. As De Pietri *et al*. (2017) remarked, "[t]his clade has repeatedly demonstrated a potential for long distance dispersal, leading to notably *Raphus* and *Pezophaps* in the Indian Ocean, and to species, or species pairs, of *Caloenas* and *Didunculus* in widespread localities in the Pacific Ocean" (p.66). This wide distribution is further increased by the referral of '*Gallicolumba*' *longitarsus* and '*G*.' *nui* to the clade. As noted by Oliver *et al*. (2023), Raphini have been largely unable to colonize Asia and "are entirely restricted to islands, despite their evident history of dispersing across vast distances into the Indian and Pacific oceans" (p.447). As such, and being largely terrestrial, raphins are particularly susceptible to human hunting.

According to Oliver *et al*. (2023, p.437), New Guinea and other Melanesian islands "have been a centre of pigeon diversification since the Eocene-Oligocene transition (~34 Mya)", with large archipelagos likely being present in the Melanesian region during the Oligocene and Miocene. Similarly, it is thought that since-submerged islands of the Mascarene Plateau were important in the dispersal of some Mascarene Island taxa (Agnarsson & Kuntner 2012). The Mascarene Plateau is thought to be 30–45 Ma (Obura 2016), with large areas (including the Saya de Malha Bank and Nazareth Bank) formerly above water (Kehlmaier *et al*. 2019). Thus, the ancestors of *Raphus* and *Pezophaps* likely dispersed from Asia (likely via the islands of the Chagos–Lakshadweep Ridge), moving south from island to island, to eventually colonize Mauritius and Rodrigues (Cheke & Hume 2008).

Caloenas is an example of a 'supertramp' taxon, with species able to colonize small or species-poor islands (McNab 2002). Comparing the raphin tree with biogeographic distribution of the clade, it appears that when raphins evolved a *Caloenas*-like morphology they were able to disperse over greater distances, leading to occupation of the Mascarene Islands in the west and the further-afield islands of the Pacific in the east. In addition, the suggestion of De Pietri *et al*. (2017) that the carpometacarpus of *Deliaphaps* shows a close resemblance to that of *Caloenas* would seem to be in accordance with Zealandia being colonized from Melanesia by a *Caloenas*-like raphin. If raphins dispersed west to east then the westerly location of *Natunaornis* (Melanesia: Fiji) might suggest a more basal placement of that taxon compared to *Bountyphaps* or '*Gallicolumba*' *nui*, which are found in the islands of eastern Pacific (Polynesia). A more basal placement would be more in accordance with Worthy's (2001) suggestion of a close relationship of *Natunaornis* to *Goura*. Likewise, the location of *Raphus* and *Pezophaps* in the Indian Ocean might suggest a more basal placement for those taxa, closer to *Caloenas*. Similarly, in the constrained trees *Bountyphaps* is resolved closer to *Raphus*, *Pezophaps* and *Natunaornis*, rather than being closer to *Didunculus* and *Caloenas* as suggested by Worthy and Wragg (2008). Homoplasy is a problem in morphology-based analyses and trees based on molecular data are often more congruent with biogeographic distributions than those based on morphological data (Oyston *et al*. 2022). The island groups where *Bountyphaps* and '*Gallicolumba*' *nui* are found are much younger than the *Raphus*-*Pezophaps* divergence date (around 20 Ma: Bruxaux 2018, figs.20, 21, supplementary fig.3). As these taxa are basal to *Raphus*+*Pezophaps* in the cladograms this represents a biogeographical incongruence.

It is unlikely that a pigeon with a morphology similar to that of *Natunaornis* or *Bountyphaps*, a flightless and a comparatively weak flyer respectively, could have dispersed to the Mascarene Islands. Therefore, the common ancestor of *Raphus* and *Pezophaps* likely retained a more *Caloenas*-like morphology. This also means that large size and terrestriality were acquired independently in several raphin lineages and that the topologies of the cladograms presented here are likely affected by homoplastic characters. Many of the smaller oceanic islands are geologically relatively recent and as such the pigeons found thereon must have either arrived by means of flight or by rafting, the latter being less likely for more isolated islands. This suggests that the taxa found on these islands were flight-capable until relatively recently. The ages of some of the more recent islands where raphins have been found are given below (data from Hembry & Balukjian 2016):

Gambier Islands and Pitcairn Islands: 0.6–5.8 Ma. Henderson Island first became emergent when sea level dropped after 380 kyr (Blake 1995), so *Bountyphaps* must have arrived subsequent to that.
Marquesas: 1.3–5.5 Ma
Samoa: 0–2.3 Ma
Society Islands: 0–4.6 Ma

The Vanuatu Archipelago emerged around 2 Ma and its biota is generally considered to have come from the Solomon Islands (Hamilton *et al*. 2010).

As for the other clades, the basalmost member of Phabini is *Starnoenas*, which has a New World distribution (Cuba). A similar circumstance is found with the Haitian cave-rail *Nesotrochis steganinos* Olson 1974 from the Caribbean, the closest relatives of which have an African and Australasian distribution (Oswald *et al*. 2021). However, in a time-calibrated Bayesian tree (Bruxaux 2018, fig.20), and in a time-calibrated tree obtained from a Bayesian analysis performed without fossils (Bruxaux 2018, supplementary fig.3A), *Starnoenas* is placed as basal to Phabini+Ptilinopodini+Raphini and basal to all pigeons except Claravini respectively. In the Oswald *et al*. (2025, fig.2) maximum-likelihood tree resulting from analysis of whole genomes, *Starnoenas* is placed as sister-taxon to Columbinae. Oswald *et al*.'s tree differs in a number of respects from those of Bruxaux and it remains to be seen whether the topology remains stable when more taxa are added. Excluding *Starnoenas* from the constrained Columbiformes and Raphini datasets in the present analyses does not affect topology.

The earliest known phabin (Late Oligocene to Early Miocene), *Primophaps*, is recorded from mainland Australia and the entire clade, with the exception of *Starnoenas*, is Australasian. The earliest known ptilinopodin (Early Miocene), *Rupephaps*, is recorded from New Zealand. The current distribution of the clade is Australasia/Pacific Ocean, southeast Asia and Indian Ocean. The Columbini are cosmopolitan, with members being found in Europe, Africa, Asia, Indian Ocean, Australasia/Pacific Ocean and the Americas. The basalmost columbins are from the Americas, as are the basalmost members of Columbiformes (in the Bruxaux 2018 tree).

Gibb & Penny (2010) remarked:

> Within pigeons, there is an asymmetric distribution of species number per genus; six of the 43 genera account for half of all pigeon species, and a third of the genera are monophyletic [...] Is this because of extinction removing diversity in many genera, as suggested by the recent discovery of extinct species of *Didunculus*, *Caloenas*, and near relatives like *Bountyphaps*, (Steadman, 2006[b])? Or is it a coincidence of success of a small number of genera, or perhaps over-classification of island variation, such as with the large flightless dodo *R. cucullatus* (Shapiro et al., 2002)? (p.705)

The authors did not explain what they meant by "over-classification of island variation" regarding *Raphus*. However, it is apparent that the diversity of raphin taxa is greater than previously thought, with new taxa being discovered from Quaternary fossil remains. The majority of raphin genera are monotypic (Gibbs *et al*. 2001), which may be related to a reduction of dispersal capability following island colonization and evolution towards increased terrestriality.

Synapomorphies and characters of *Raphus*+*Pezophaps* (Raphina)

The unambiguous synapomorphies of Raphina (*Raphus*+*Pezophaps*) are: ratio of carpometacarpus length to humerus proximal width <1.3 and pisiform process of carpometacarpus absent (or greatly reduced). These characters are probably related to loss of flight and thus were probably acquired independently, in which case they would not be true synapomorphies. An additional synapomorphy is the ratio (0.38) of the distance from the distal end of the tarsometatarsus to the proximal margin of the fossa metatarsi I to the total length of the tarsometatarsus. However, this ratio differs only slightly in *Natunaornis* (0.37). A distinctive bow-shape of the horizontal semicircular canal, seen in both *Raphus* (Gold *et al*. 2016) and *Pezophaps* (unpublished CT data from Larry Witmer, personal communication), may also be a synapomorphy of these two taxa, although a weak bow-shaped curvature is also seen in *Goura cristata* and *Chalcophaps indica* (Linnaeus 1758) (Gold *et al*. 2016) and data is lacking for the other extinct raphins.

Using the present cladograms, characters for which data are absent for *Raphus* and *Pezophaps* can be extrapolated. Thus, it is hypothesized that they possessed the following features: wing diastataxic, aftershaft present, uropygial gland naked or absent (note: there is no relationship between flightlessness and loss of the uropygial gland: Johnston 1988), caeca absent, plantar tendons of pes of type I, sterno-tracheal muscles asymmetrical, spinal chord leiocerate, gallbladder absent.

Evolution

Raphin taxa show a general increase in body mass, from *Trugon* (323–400 g) to *Raphus* (*c*.8,000–20,000 g) and *Pezophaps* (14,860–27,500 g: Parish 2013). However, there appears to be convergence in large body mass, with *Goura* attaining a mass of over 1 kg, also seen in *Raphus*, *Pezophaps* and *Natunaornis*. All of the major clades of Columbidae (Raphini, Phabini, Ptilinopodini and Columbini), with the exception of Claravini, have members with large body mass (>400 g), although Raphini shows the greatest tendency towards large size (see Appendix 5 for columbid body mass data). Non-raphin columbids with body mass over 400 g include members of *Columba*, *Ducula*, *Leucosarcia* Gould 1843 and *Lopholaimus*. It is also of note that the basalmost columbids (as identified from molecular analyses: *Claravis* Oberholser 1899, *Uropelia* Bonaparte 1855a, *Metriopelia* Bonaparte 1855a and *Columbina* Von Spix 1825) are all small (<130 g mass). There is some indication that the island rule (see Benítez-López *et al*. 2021; Jezierski *et al*. 2024) applies to raphins, with larger taxa found on larger islands, although there are some exceptions, such as *Trugon*.

Raphus and *Pezophaps* show numerous features, some of which are also seen in other raphins, which are likely the result of heterochronic evolution (see Appendix 6). However, it is not always easy to determine whether a feature is due to heterochrony, particularly as there is little data on the ontogeny of columbiform taxa.

Natunaornis is placed as sister-taxon to *Raphus+Pezophaps* in the analyses. This may be representative of the actual relationship or it may be due to the effects of convergent features relating to flight loss and increased body size. Given the great distance between the Pacific islands (where *Natunaornis* and *Bountyphaps* are found) and the Mascarenes (where *Raphus* and *Pezophaps* are found) it is most likely that flight loss occurred independently. Furthermore, the numerous differences between *Raphus* and *Pezophaps* suggest that these genera also became flightless independently.

Pneumatization

Members of the clade Raphini (including the smaller taxa) show greater pneumatization than other columbids, and some are also amongst the heaviest columbids, with *Raphus*, *Pezophaps* and *Natunaornis* being the largest of all the family. Indeed, there appears to be a relationship between the degree of pneumatization and body mass, with many of the taxa of body mass ≥400 g having pneumatization of the scapula, omal end of the coracoid, incisura capitis of the humerus, and the femur. Furthermore, the degree of pneumatization in birds does not appear to be linked to flight ability: ratites have well-pneumatized bones, and hornbill bones are very pneumatized (Bellairs & Jenkin 1960). A pneumatic foramen on the cranial face of the proximal femur (illustrated in Figure 7) is found in all raphins over 500 g (with the exception of *Otidiphaps*), and also in the ptilinopodin *Megaloprepia* Reichenbach 1853 (body mass 250–470 g). A positive relationship between body size and relative pneumaticity has been suggested (Bellairs & Jenkin 1960; McLelland 1989; Müller 1908), and many large flightless birds have pneumatized femora, including *Struthio* (Bezuidenhout *et al*. 1999), *Dromaius* Vieillot 1816, *Dinornis* Owen 1843, *Dromornis* Owen 1872, *Megavitiornis* Worthy 2000 and *Sylviornis* Poplin 1980 (Worthy *et al*. 2016). However, O'Connor (2004) observed that in Anatidae (excluding diving taxa) although there is a positive relationship between body size and relative pneumaticity, this is low and that factors other than body size are involved. Similarly, Gutherz & O'Connor (2022) noted that "body mass and pneumaticity exhibit a positive relationship, although this relationship is often overridden by other life histories (e.g., locomotor specializations), and/or phylogenetic factors" (p.1396).

Pneumatization of the femur in cursorial species is also seen in Cuculidae (members of Columbaves, along with Otidiformes, Musophagiformes, Columbiformes, Pterocliformes, Mesitornithiformes: Stiller *et al*. 2024), with a pneumatized femur being present in Neomorphinae and also in the large and generally terrestrial *Centropus goliath* Bonaparte 1850 (Gutherz & O'Connor 2021). Gutherz & O'Connor (2021) remarked that "[f]unctionally, pneumatizing the femur may represent a response to increased biomechanical loads" (p.5), which may also be the case in Raphini.

There is a general increase in pneumaticity in successive taxa along the branch leading to *Raphus*. For example, a pneumatic fossa in the incisura capitis of the humerus is seen in derived raphins (*Goura* and *Caloenas*>*Raphus*). Pneumatization of the humerus appears to develop relatively late in birds (Burton *et al*. 2023) and it could be speculated that an extended growth period allowed further pneumatization to occur, the larger species of a family often having low rates of growth and prolonged growth periods (Ricklefs 1968). *Raphus* itself shows much skeletal variation (Parish 2020), which may have occurred late in development (see Appendix 6 for some examples). Angst *et al*. (2017, p.4) stated that the Dodo grew rapidly until it reached sexual maturity, after which "it took several years to attain skeletal maturity", as indicated by the presence of lines of arrested growth (LAGs) in its bones.

The bones of *Pezophaps* show less pneumaticity than might be expected given its large size and phylogenetic placement. Its bones generally also have a more smooth appearance than those of *Raphus*, with muscle impressions being less well marked. The less pneumatic condition of the skeleton of *Pezophaps* may have been beneficial in intraspecific combats, with less pneumatic bones potentially being stronger (more resistant to physical trauma) than strongly pneumatized ones. However, this hypothesis requires evaluation.

Increase in size of the foramen orbitonasale laterale

The foramen orbitonasale laterale is large in most Raphini (see Figure 7 for illustration; its form is unknown for *Bountyphaps*, *Microgoura*, *Natunaornis*, '*Gallicolumba*' *longitarsus* and '*G*.' *nui*), compared with that of other columbids. In *Raphus* it is secondarily reduced by expansion of the lacrimal and ectethmoid. The increase in size of the foramen may be linked to paedomorphism (a larger foramen being seen in juvenile pigeons; pers. obs.), and a large foramen is also seen in members of the proximal outgroup Pteroclidae (*Pterocles* Temminck 1815, *Nyctiperdix* and *Syrrhaptes* Illiger 1811). This may also be related to the presence of unfused lacrimals in some specimens of *Raphus* (Thirioux's Port Louis skeleton: Claessens *et al*. 2015; Parish 2020) and *Pezophaps* (NHMUK PV A.1454 and A.1373). The basal raphin *Trugon* has a relatively small orbitonasal foramen.

Number of cervical and synsacral vertebrae

There is an increase in the number of cervical vertebrae in many raphins, from fourteen (in most non-raphins) to fifteen or sixteen (the condition in *Trugon* is unknown, as is the case for several extinct taxa; *Didunculus* only has fourteen

cervicals). This is also seen in *Starnoenas* and in some specimens of *Phaps* and *Ducula*, as well as in the outgroup taxa (Pteroclidae, Mesitornithidae and Megapodiidae), which are all (*Ducula* excepted) terrestrial. *Raphus* also appears to have an extra cervical vertebra (Claessens *et al*. 2015): (almost) all other columbids have eighteen presacral vertebrae (Verheyen 1957), whereas *Raphus* has nineteen.

Likewise, there is a general increase in the number of synsacral vertebrae, with the largest species (for which data are available: *Raphus*, *Pezophaps* and *Goura*) having seventeen or more, and larger pigeons (*Raphus*, *Caloenas*, *Goura*, *Otidiphaps*, *Starnoenas*) and outgroup taxa having at least sixteen. This is likely linked to an increase in terrestriality.

Morphology of basal raphins

The basal raphins *Otidiphaps* and *Trugon* show a narrow sternum and elongate lateral processes, with a Sternal Index (see Appendix 3) of > 2 (the sternum is unknown for *Microgoura*). This sternal morphology is also seen some phabins (*Geopelia*, *Geophaps*, *Leucosarcia* and *Starnoenas*) and a similarly elongate sternum is also seen in tinamous (Verheyen 1960). *Goura* also has a relatively elongate sternum (Sternal Index 1.75–2.00), although not as elongate as in the above taxa. A narrow caudal border of the sternum and related narrower trunk appears to be linked to increased terrestriality (Lowi-Merri *et al*. 2021).

Otidiphaps and *Trugon* also have comparatively long hindlimbs relative to forelimbs, with a Locomotory Index (see Appendix 3) of <0.8. Again, this is also seen in some phabins: *Leucosarcia* 0.8, *Starnoenas* 0.72–0.76, *Gallicolumba luzonica* Scopoli 1786 0.74, as well as in tinamous (0.71–0.88; Verheyen 1960). Steadman & Takano (2020) remarked: "The overall curvature of the femur in *Otidiphaps* is reminiscent of that in *Ortalis* [Merrem 1786] or *Penelope* [Merrem 1786] (Galliformes, Cracidae). Both cristae cnemialis are also very well developed. Relative to its forelimb elements, the hindlimb bones of *Otidiphaps* are longer than in any extant columbid. Taken together, these characters may be adaptations for efficient walking or running on tree limbs and on the ground" (p.404). In addition, both *Otidiphaps* and *Trugon* are eutaxic, as are phabins. Basal raphins (*Microgoura*, '*Gallicolumba*' *longitarsus*, *Otidiphaps* and *Trugon*), as well as some more derived taxa (*Goura* and '*G*.' *nui*) have elongate tarsometatarsi (length to proximal width > 5), as also seen in many phabins (*Gallicolumba*, *Geopelia*, *Geophaps*, *Phaps* and *Starnoenas*). These characters all suggest that the last common ancestor of Raphini, Ptilinopodini and Phabini was phabin-like.

Placement of *Gallicolumba longitarsus* and *G. nui*

In the results of the constrained Raphini analysis, '*Gallicolumba*' *longitarsus* is resolved as sister-taxon to *Microgoura*. It differs from *Microgoura meeki* in size (tarsometatarsus length 51.6 mm compared to 58.7 mm in *M. meeki*) and in that the proximal width of the tarsometatarsus is greater than the distal width (the reverse is true for *M. meeki*). There are also slight differences in tarsometatarsal proportion: the ratio of length to proximal width being 6.37 (6.45 in *M. meeki*); the ratio of length to distal width being 6.53 (6.11 in *M. meeki*). '*G*'. *longitarsus* might represent a second species of *Microgoura* (*M. longitarsus*), although this conclusion is, at present, tentative and further anatomical comparisons are needed to confirm or refute this conclusion.

In the results of the constrained Raphini analysis, '*Gallicolumba*' *nui* is placed basal to *Bountyphaps*. The clade '*Gallicolumba*' *nui* > *Raphus* is defined by a number of character states: the procoracoid lobe of the coracoid not extending craniad of scapular cotyla, the medial angle of the coracoid being acute, and the humeral head not projecting (or projecting only slightly) beyond a line marking the proximal margin of the incisura capitis.

Two other species assigned to *Gallicolumba* might also belong in Raphini – more if the records attributed to '*Gallicolumba*' *nui* from the Society Islands and the Cook Islands are distinct taxa as would seem likely for these apparently weak-flying, if not flightless, taxa (Trevor Worthy, personal communication). Steadman, (1992a, p.79) mentioned a new species of *Gallicolumba* from Rota, Mariana Islands: "The giant ground-dove, *Gallicolumba* new sp., is represented by a mandible, tarsometatarsus, and pedal phalanx (USNM 436623, 436660, 436588). It is most similar in size and other features to the largest species in the genus, *Gallicolumba* new sp. [= '*G*'. *nui*] from East Polynesia." This taxon was still referred to *Gallicolumba* by Steadman (2006b).

Meredith (1991, pl.5) figured a partial coracoid and a distal end of tarsometatarsus of a columbid from Norfolk Island, which he labelled as "*Gallicolumba* prob. *norfolciensis*". However, this taxon may be more closely related to *Pampusana stairi* (Trevor Worthy, personal communication). Whether these specimens belong in *Gallicolumba* (or *Pampusana*), or whether they belong elsewhere, perhaps in Raphini, awaits further investigation.

Conclusion

The results of the present unconstrained analyses confirm that *Raphus* and *Pezophaps* are members of the columbiform subfamily of terrestrial pigeons including *Otidiphaps*, *Trugon*, *Didunculus*, *Goura* and *Caloenas*. The placement of the Dodo and Solitaire also allows the extrapolation of certain soft tissue features unknown from preserved remains.

The Dodo and Solitaire have now been placed into a wider context as the largest members of a clade of terrestrial pigeons (including at least one other flightless species). However, the exact relationships between the raphin taxa remain uncertain. As is increasingly often found, areas of conflict with the results of molecular phylogenetic analyses suggest that the unconstrained results may not be representative of evolutionary history, due to the restrictions of the data and the analysis. However, the use of a molecular-based constraint does allow a more robust assessment of taxa not known from molecular data, and here the relationships of several fossil/extinct taxa are phylogenetically assessed for the first time. Due to the presumed convergences associated with increased terrestriality and associated increase in size and loss of flight ability, the preferred trees are those constrained using the molecular backbone of Bruxaux (2018; see above).

It is apparent, from both the molecular and the present morphological analyses, that increased terrestriality evolved more than once within Columbidae. Apart from Raphini, it is also particularly apparent in phabins such as *Gallicolumba*. As there is a tendency towards increased terrestriality in Columbidae, associated with the colonisation of islands, morphological convergence between different lineages makes accurate character-based phylogenetic reconstruction difficult.

The recognition of '*Gallicolumba*' *longitarsus* and '*G*.' *nui* as raphins adds to both the diversity and geographical distribution of that clade and further confirms that raphins are exclusively island taxa. Basal members of Raphini are already terrestrial, although greater capacity for dispersal was acquired with the evolution of a *Caloenas*-type morphology, allowing more distant islands to be colonized.

Supplementary Data

Supplementary data for this article can be accessed online at
https://archive.org/details/dodo-phylogenetic-analysis-supplementary-data-parish-2025
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[Note: This article is essentially the same as that published on the *Historical Biology* website (25th March 2025: https://doi.org/10.1080/08912963.2025.2473546), except for minor differences: in style and format and in the absence of the errors introduced during the proof-creation process and not corrected in the published version. In addition, a couple of other errors have been corrected: Sharpe (1893) (in the caption to fig.5) emended to Salvadori (1893); “Meredith (1991, p.1)” [“Meredith (1991, pl.1)” in the pre-proof text] emended to “Meredith (1991, pl.5)”. DOI numbers for texts widely considered to be Public Domain have also been omitted, as these refer to copies of publications occluded by a paywall. These texts can be found unoccluded at the Internet Archive and other sites.

Jolyon C. Parish, March 2025

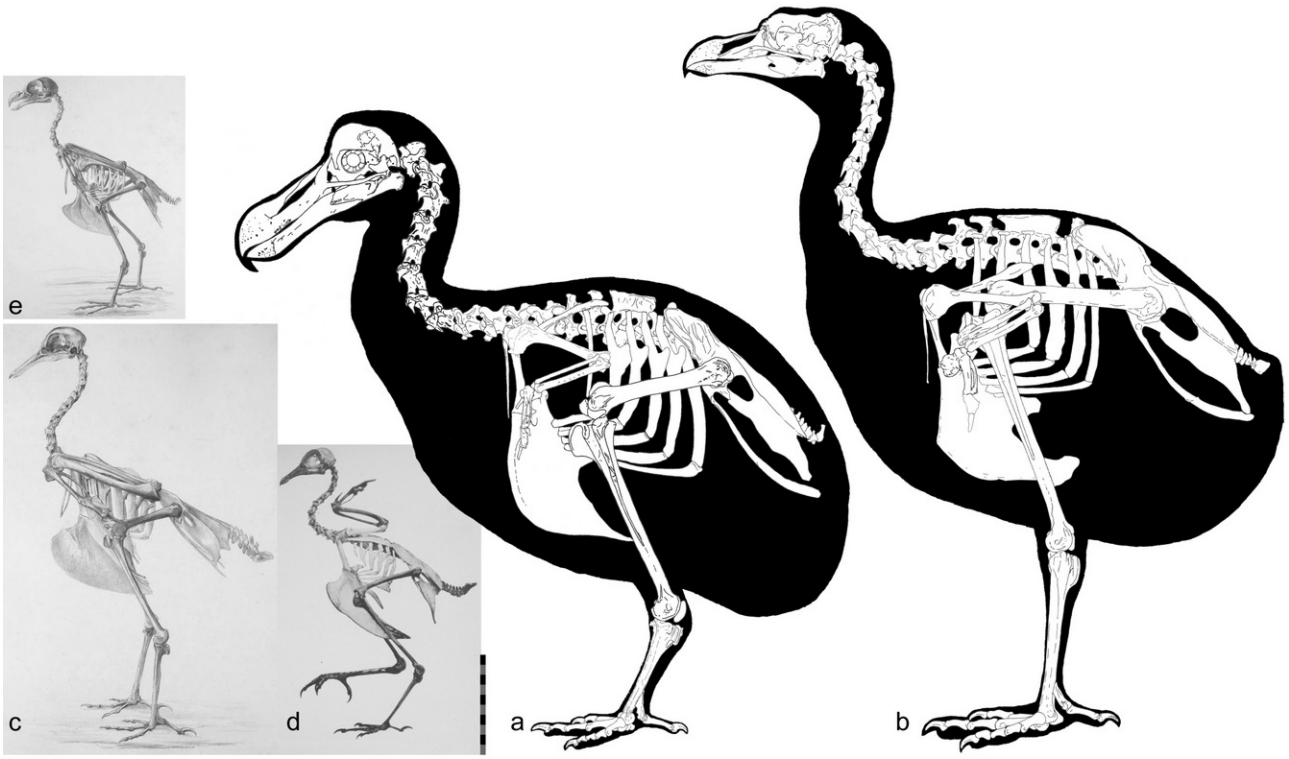

Figure 1: Reconstructed skeletons of the dodo (*Raphus cucullatus*; a) and male solitaire (*Pezophaps solitaria*; b) with body outlines added (from Parish 2020), compared with the skeletons of extant pigeons: c: *Goura cristata* (Eyton 1867, pl.1.G), d: *Otidiphaps nobilis* (Meyer 1879–1888, Band I, Tafel viii), e: *Didunculus strigirostris* (Eyton 1869, pl.22). Scale in cm.

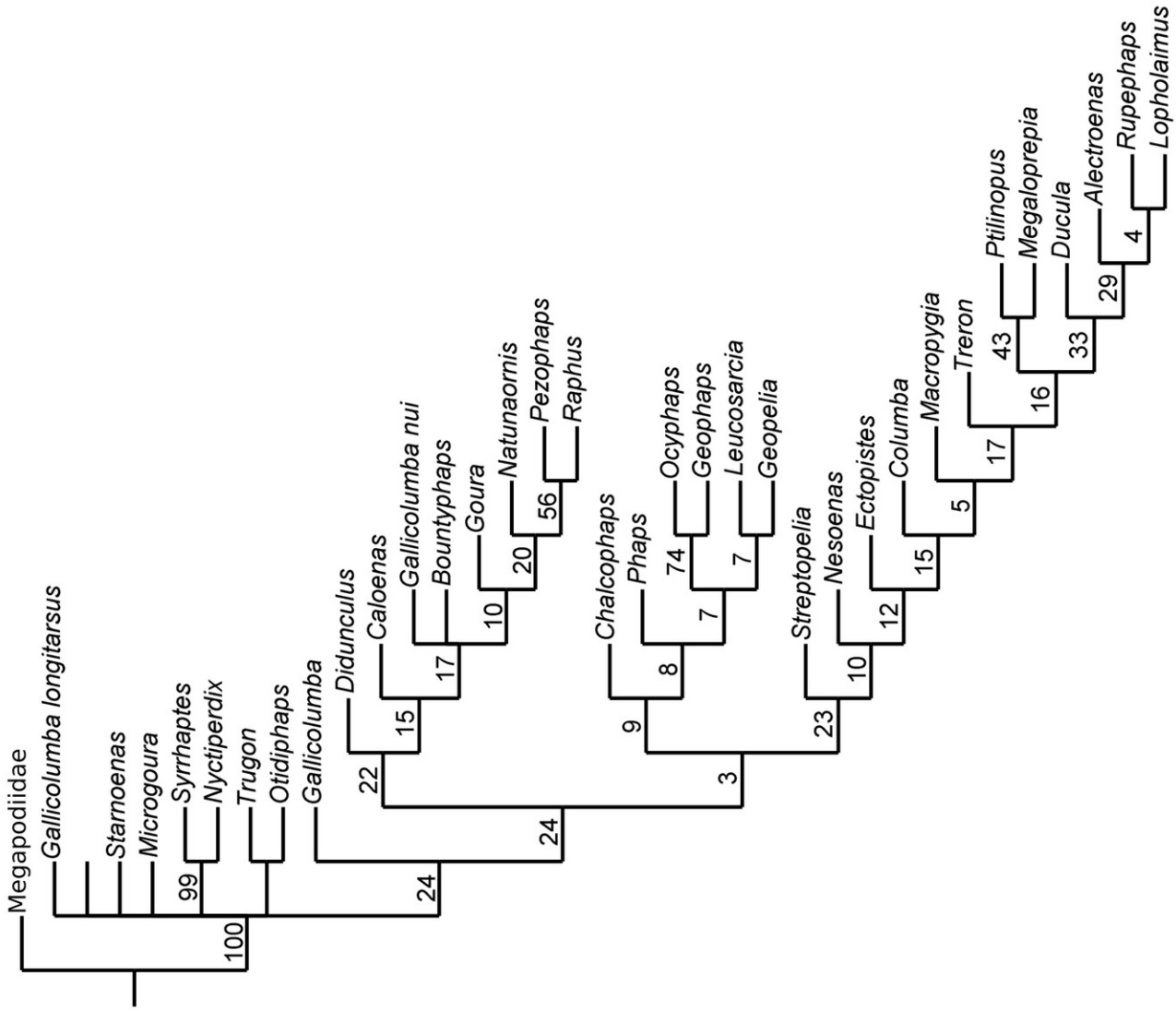

Figure 2: Strict consensus of 4 MPTs (score 484.379) of the unconstrained Columbiformes data set. Numbers are bootstrap support values (10000 replicates).

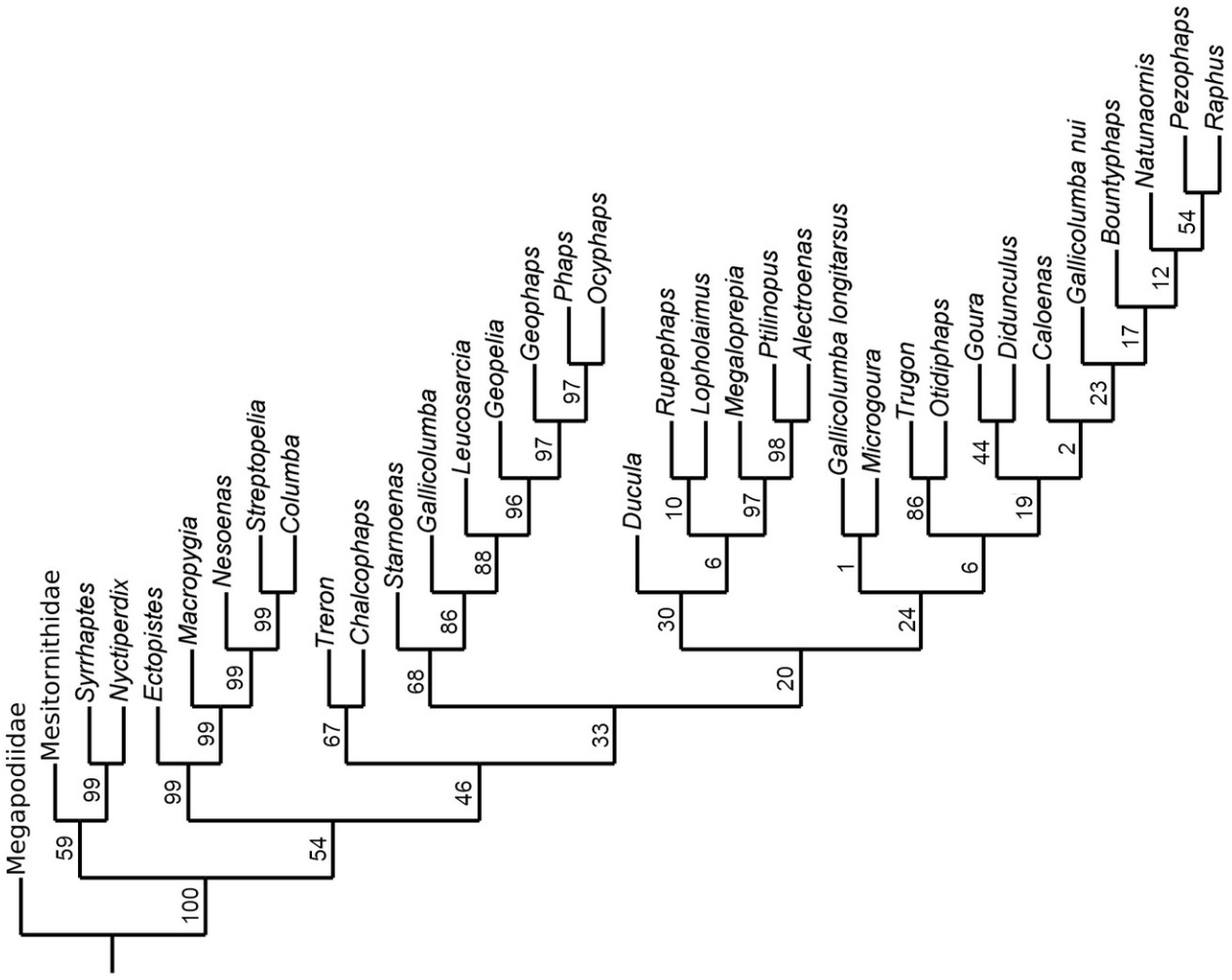

Figure 3: Single MPT (score 547.150) resulting from analysis of the constrained Columbiformes data set. Numbers are bootstrap support values (10000 replicates).

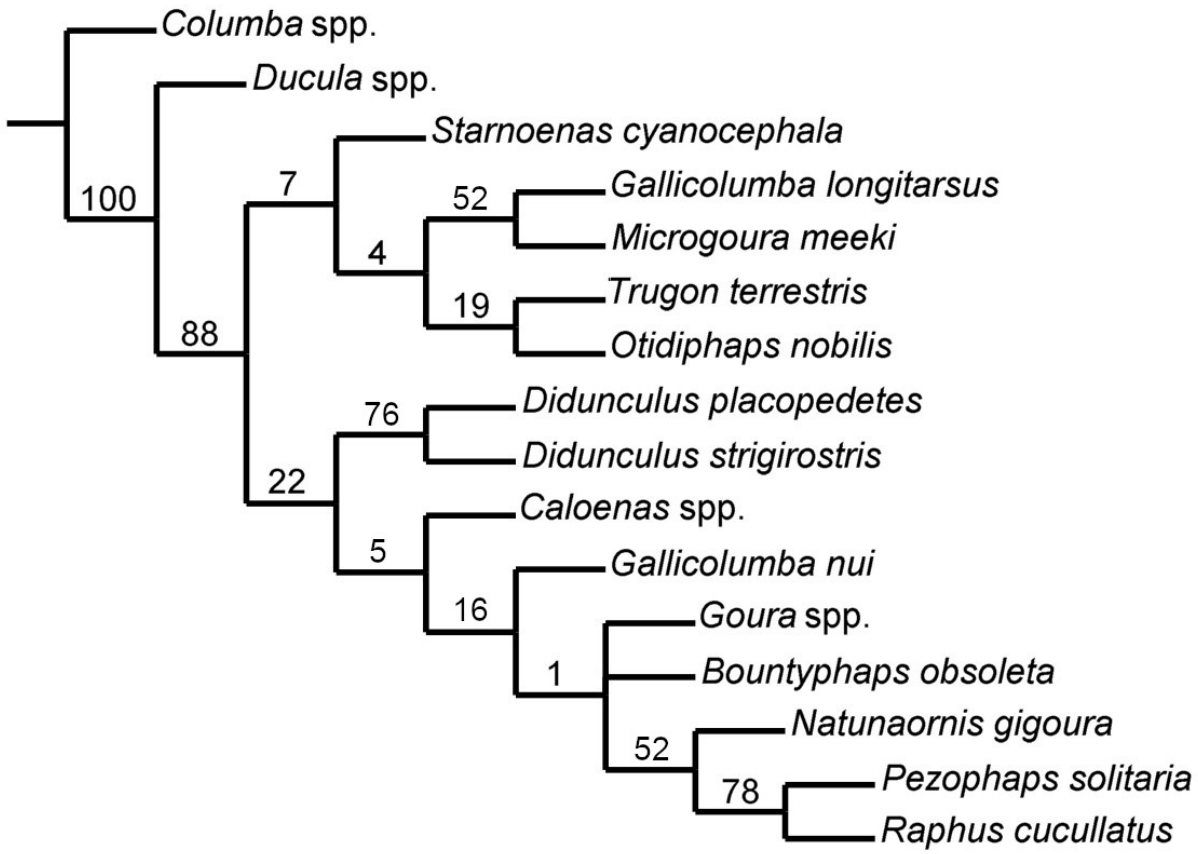

Figure 4: Strict consensus of 2 MPTs (score 223.880) of the unconstrained Raphini data set. Numbers are bootstrap support values (10000 replicates).

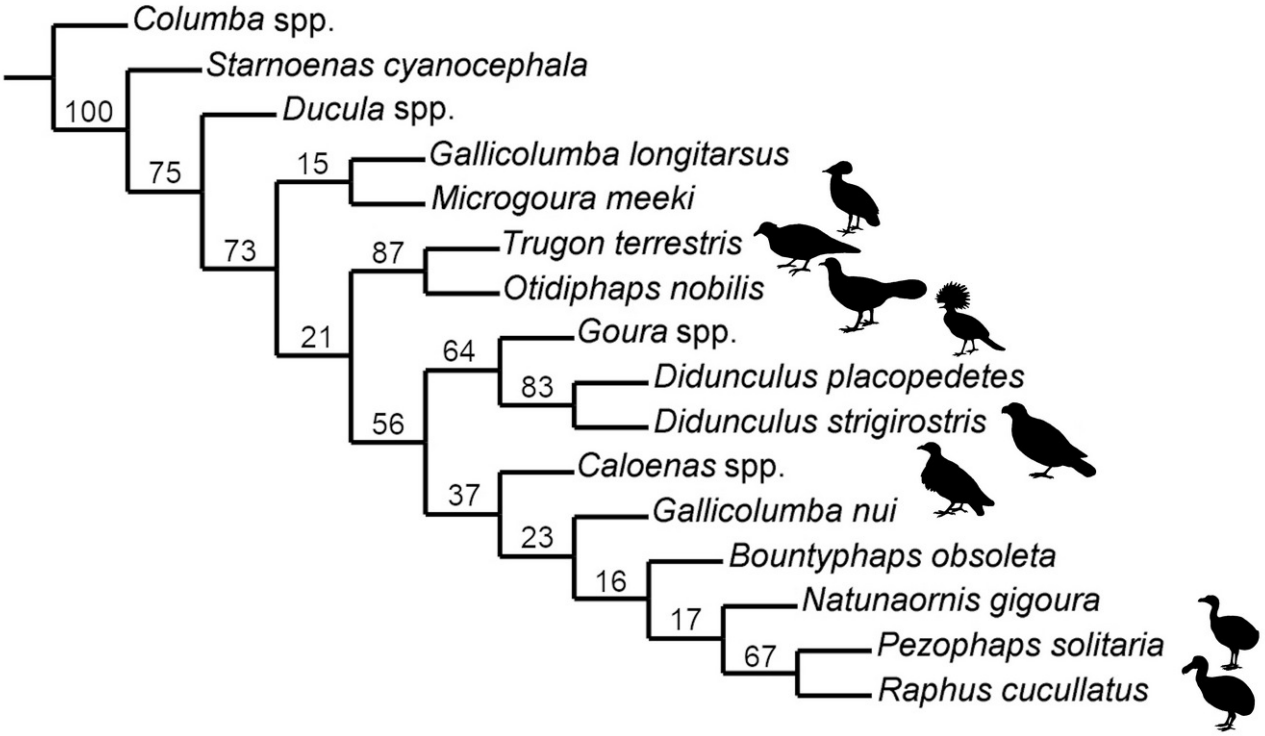

Figure 5: Single MPT (score 241.000) resulting from analysis of the constrained Raphini data set. Numbers are bootstrap support values (10000 replicates). Silhouettes of raphin taxa (not to scale) modified from the following sources: *Microgoura*: Keulemans (1904); *Trugon*: Gould (1875–1888); *Otidiphaps*: Salvadori (1893, pl.xv); *Goura*: (Finsch 1875, pl.lxviii [*G. scheepmakeri*]); *Didunculus*: Brehm (1882); *Caloenas*: E. C. S. Baker (1913, pl.10); *Raphus* and *Pezophaps*: Jolyon C. Parish.

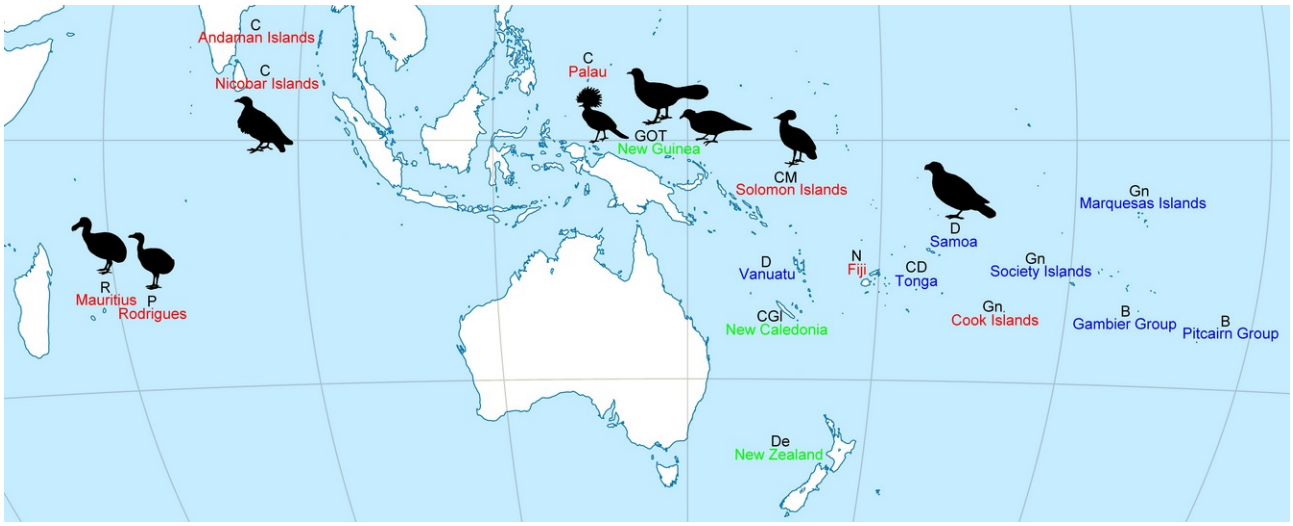

Figure 6: Geographic distribution of Raphini. Abbreviations: B: *Bountyphaps*, C: *Caloenas*, D: *Didunculus*, De: *Deliaphaps*, G: *Goura*, Gl: "*Gallicolumba*" *longitarsus*, Gn: "*Gallicolumba*" *nui*, M: *Microgoura*, N: *Natunaornis*, O: *Otidiphaps,* P: *Pezophaps*, R: *Raphus*, T: *Trugon*. Key to age of the oldest emergent land within the named group: green = >30 Ma, red = 7-30 Ma, blue = 0-6 Ma. Sources for island ages: New Guinea: Harrington *et al.* (2017); New Caledonia, Solomon Islands: Keppel *et al.* (2009); New Zealand: Sharma & Wheeler (2013); Mauritius, Rodrigues: Agnarsson & Kuntner (2012); Andaman Islands, Nicobar Islands: Srivastava *et al.* (2021); Palau: Keppel *et al.* (2024); Fiji, Tonga: Worthy & Burley (2020); Cook Islands: Turner & Jarrard (1982); Vanuatu: Hamilton *et al.* (2010); Gambier Group, Pitcairn Group, Marquesas, Samoa, Society Islands: Hembry & Balukjian (2016). Silhouettes as in fig.5 (not to scale). Base map: TUBS, supported by Alexrk2; Creative Commons Attribution-Share Alike 3.0.

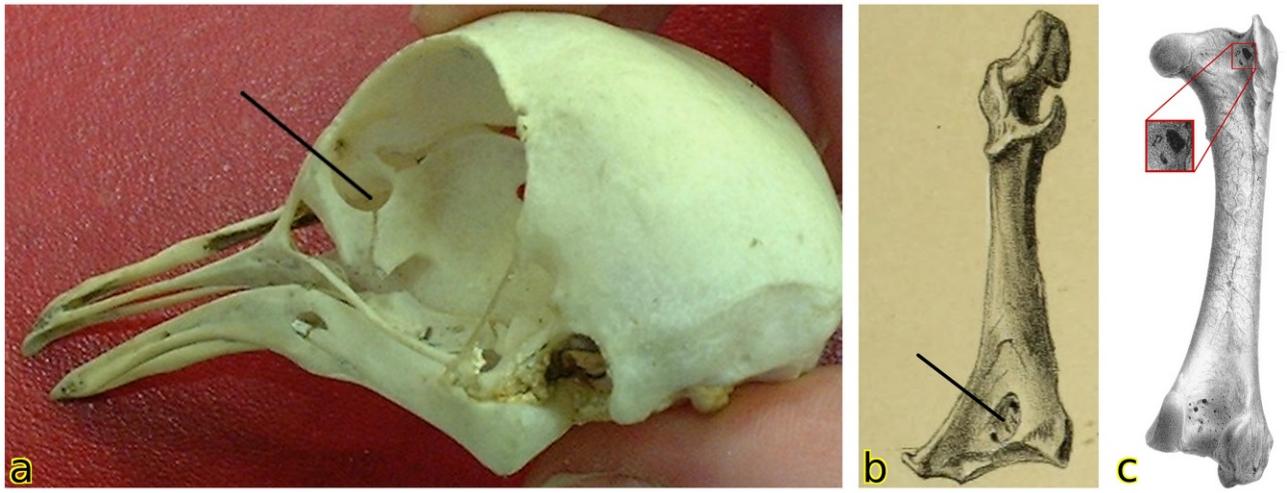

Figure 7: Selected raphin features mentioned in the text: a) large foramen orbitonasale laterale (arrowed; *Goura cristata* UMZC 413.B1; Jolyon C. Parish), b) centrally-located pneumatic fossa in the supracoracoid impression of the coracoid (arrowed; *Caloenas nicobarica*: after Milne-Edwards 1869–1871, pl.139, fig.8), c) pneumatic foramen on the cranial face of the proximal femur (*Raphus cucullatus*: after Owen 1867, pl.xxi, fig.1).